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Upland Forest Linkages to Seasonal Wetlands: Litter Flux, Processing, and Food Quality

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Abstract

The flux of materials across ecosystem boundaries has significant effects on recipient systems. Because of edge effects, seasonal wetlands in upland forest are good systems to explore these linkages. The purpose of this study was to examine flux of coarse particulate organic matter as litter fall into seasonal wetlands in Minnesota, and the relationship of this flux to development of mosquitoes (*Aedes aegypti*). We hypothesized that litter flux into seasonal wetlands was dominated by upland plant litter that was lower quality and slower to breakdown than wetland litter, and that development rate of mosquitoes reared on upland litter was less than those reared on wetland litter. Of total litter fall into the wetlands, 71% originated in upland forest. Carbon to nitrogen ratios differed between upland litter (mostly sugar maple (*Acer saccharum*) and trembling aspen (*Populus tremuloides*) leaves) and wetland litter (mostly black ash (*Fraxinus nirgra*) leaves), averaging 63.9 and 47.7, respectively over two years. Breakdown rate of black ash leaves was faster than upland leaves (k (day^{-1}) = 0.00329 and 0.00156, respectively), based on the average between wetland margins and centers. Development of mosquito larvae fed black ash leaves was faster than larvae fed upland leaves. Our results demonstrate linkages between upland forests and seasonal wetlands through litter fall. The abundance of upland litter in the wetlands may influence litter breakdown and carbon assimilation by invertebrates. Wetlands receiving high amounts of upland versus wetland litter may be lower quality habitats for invertebrates that depend on detrital pools for their development.

Key words: seasonal wetlands; ecosystem linkages; forest wetlands; CPOM; litter flux; litter breakdown; wetland invertebrates.

Introduction

The flux of energy, materials, and organisms across ecosystem boundaries can have significant effects on the function and dynamics of recipient systems (Junk and others 1989; Polis and others 1997; Wallace and others 1997; Rose and Polis 1998; Helfield and Naiman 2001). Seasonal wetlands embedded in upland temperate forest are good model systems to explore such linkages, but they have not been examined from this perspective. Many seasonal wetlands are small (generally <2000 m^2; Palik and others 2001) and the potential for linkage to the surrounding system is high due to increased perimeter to area ratios and heightened edge effects. Seasonal wetlands also support distinctly different plant and animal communities than the surrounding upland forest. Consequently, inputs from the adjacent forest are likely to be different in character than those produced internally. Finally, seasonal wetlands are abundant and hence cumulatively important ecologically in many landscapes and regions (Brooks and others 1998; Palik and others 2003).

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We explored linkages between seasonal wetlands and upland forests as mediated by the flux of coarse particulate organic matter as litter fall from the forest to the wetlands. We hypothesized that because of small wetland size, and high perimeter to area ratios, litterfall into seasonal wetlands would be dominated by upland tree sources. We were also interested in the effects of upland derived litter on wetland function. To that end, we compared litter quality and breakdown rates between upland derived litter and that produced in the wetland. The wetlands we studied are dominated by black ash (*Fraxinus nigra* Marsh.). Previously published values of breakdown rates for this species suggest higher litter quality relative to many upland forest species (Petersen and Cummins 1974). We hypothesized that upland derived litter would be of lower quality, as measured by carbon to nitrogen ratio (C/N), and slower to decompose, than wetland derived black ash litter. Finally, we examined survival and development of mosquito larvae reared on upland versus wetland derived leaf litter. We hypothesized that larvae reared on upland litter would have reduced survival and impaired development relative to those raised on wetland derived litter.

Study Area and Wetland Selection

We conducted our study within the Sucker Lakes watershed on the Chippewa National Forest in northern Minnesota, USA. Upland forests of the study area consist of northern hardwood ecosystems dominated by sugar maple (*Acer saccharum* Marsh.), with lesser amounts of basswood (*Tilia americana* L.), trembling aspen (*Populus tremuloides* Michx.), bigtooth aspen (*P. grandidentata* Michx.), paper birch (*Betula papyrifera* Marsh.), and ironwood (*Ostrya virginiana* (Miller) K. Koch) (Chippewa National Forest 1996). The dominant woody plant species in the wetlands is black ash, along with small amounts of speckled alder (*Alnus rugosa* (Duroiu) Sprengel) and American elm (*Ulmus americana* L.) (Palik and others 2001, 2003).

In 1996, United State Forest Service staff identified all seasonal wetlands in the watershed using 1:15,850 leaf-off, color infrared aerial photography. We selected four wetlands randomly from this population and determined their appropriateness for the study based on the following criteria: (a) the surrounding upland forests were at least 70 years of age (based on Forest Service records); (b) wetlands and the surrounding forests showed no evidence of recent disturbance since the last harvest; (c) wetland area was between 200 and 3000 m^2; (d) wetlands had mucky, mineral soil substrates, as opposed to peat; (e) at the time of selection in spring 1997, water depth in the basins was at least 0.1 m; and (f) wetland tree communities were dominated by black ash, with high tree canopy cover (canopy cover of trees over the selected wetlands ranged from 87 to 96%; Palik and others 2001). Wetlands not meeting these criteria were rejected and another was selected randomly. The study wetlands conform to the definition of a seasonal wetland following Cowardin and others (1979), as palustrine, forested wetlands having a semipermanent or seasonally flooded water regime and a mineral soil substrate.

Mean (±sd) hydroperiod (average consecutive days with water in 1998 and 1999) of the wetlands was 136 ± 37 days, as measured from approximately April 1 to November 1 (Palik and others 2001). Maximum and mean depths (average of 1998 and 1999, as determined by bi-weekly staff gage readings) were 0.80 ± 0.37 and 0.39 ± 0.16 m, respectively (B. Palik, unpublished data). The wetlands are inundated in the spring from snowmelt and water levels are maintained by spring and early summer rain events. In each wetland, water was largely confined to a well defined basin. We saw no evidence for flooding of the adjacent forest, outside of this basin. The wetlands are isolated hydrologically from surface connections with other wetlands and aquatic systems. Potentially, there is some seasonal groundwater discharge into the wetlands, although this has not been explored for our study sites.

Methods

Litter Flux and Quality

In each wetland 9 to 12 gravity collectors were placed in 1997 and 1998 to collect litter input. In 1998, we added six traps around each wetland that were designed to estimate the lateral movement (from wind or surface water flow) of litter from the uplands into the wetlands. Gravity traps consisted of wire tomato cages lined with mesh funnels and had surface areas of 0.19 m^2. The legs of the traps were pushed into the wetland substrate or into lengths of PVC pipe that were anchored into the substrate. Lateral traps consisted of rectangular wooden boxes (0.46 × 0.20 × 0.20 m) that were open on two opposing (long axis) sides. One opening was covered with wire mesh. Lateral traps were placed on the ground inside the wetland basin within 1 m of the wetland margin, with the open end facing the upland. Litter was collected monthly from April through early September and bi-weekly from early September until early November. The April collection included any litter falling between the last November collection and the first collection in April. Most litter in the wetlands and upland falls between mid-September and mid-October. Litter flux was measured as g m^{-2} y^{-1} or g m^{-1} y^{-1} for gravity and laterally deposited litter, respectively.

Leaf litter was dried at 65°C for 48 h, sorted by species and tissue type (that is, leaf, twig), and weighed. Samples were ground using a Wiley Mill. Litter subsamples (5 to 25 mg), along with several standards (alfalfa Ar2018, rice flour Ar2028), were analyzed using a Carlo Erba C/N Analyzer to determine carbon and total nitrogen concentrations.

Leaf Litter Breakdown

Leaf litter breakdown was measured in 1998–1999 in both the wetland centers and margins. Species of litter included black ash, sugar maple, and trembling aspen. We included the former two species because they are the most abundant wetland and upland tree species in the study area, respectively, and the latter species because it is an important early successional tree that often increases in abundance when forests of the region are harvested. Litter bags were constructed by sewing two 15 × 15-cm layers of 5-mm mesh together. Fresh, recently abscised leaves were collected in fall 1998. Each bag contained approximately 4 g of fresh leaves from one species. Initial leaf dry mass and ash content were determined from subsamples dried in an oven at 60°C for 48 h and combusted in a muffle furnace at 525°C for 2 h.

We placed 48 bags of each species in each wetland in the fall 1998. An equal number of bags were distributed in the wetland centers and the margins. Three bags of each species were retrieved from the two locations after 14, 28, 204, 243, and 361 days of exposure. We did not estimate handling loss by retrieving bags immediately after placement in the wetlands. After retrieval, the litter was gently washed and cleaned of invertebrates and debris. The litter was oven-dried and weighed, and ash content was determined on subsamples. Invertebrates from the litter bags were not identified.

Feeding Bioassay

We conducted two laboratory bioassays using *Aedes aegypti* mosquito larvae to assess the relative qualities of different leaf species as invertebrate food. The source colony for the larvae is housed in the Department of Entomology at the University of Georgia. Laboratory studies were used instead of field studies because food quality cannot be manipulated in isolation in the field (abiotic conditions will also vary). We used *A. aegypti* because none of the mosquito species native to the study wetlands (Batzer and others 2004) were available in colony form. Two additional invertebrate genera endemic to the wetlands, *Chironomus* and *Daphnia*, were available in laboratory colonies. However, *Aedes* was considered the most useful of the three because of adaptations that allow *Aedes* to breath from the atmosphere, and we were concerned the effects of litter decomposition on dissolved oxygen would affect feeding rates of *Chironomus* and *Daphnia*. Additionally, *Aedes aegypti* was a useful test organism because it normally completes development from egg to adult in a short period (~7–14 days), reducing problems with extraneous variation in habitat quality that may develop over time. However, because we used an invertebrate that was not native to the wetlands, our study was designed only to develop an index of food quality among different litter types, and extrapolation of results to temperate wetlands must be done with caution.

For the first bioassay, we used sugar maple, black ash, and trembling aspen leaves. We added 0.4 g of oven-dried leaf litter from each species to petri dishes containing 40 ml of deionized water ($n = 9$ for each treatment); deionized water is similar in chemistry to precipitation that naturally fills the wetlands. Leaves were conditioned in petri dishes for two weeks to establish fungal and bacterial biofilms. Conditioning is necessary because most aquatic invertebrates do not feed on leaf matter directly but instead browse on surface biofilms (Cummins and others 1989). Fungal and bacteria growth was visible on the leaves after the 2-week conditioning period, and thus biofilms should have occurred in sufficient quantity to support the small numbers of mosquito larvae used in each trial replicate. At that time, five second instar larvae were added to each of the petri dishes.

A fourth (control) treatment provided high quality food conditions to the developing larvae. In this treatment ($n = 9$), five larvae were added to deionized water containing ground commercial dog food plus yeast (this is the standard food used for mosquito colony maintenance at the University of Georgia). The food was added in small amounts throughout the experiment so that it was never limiting.

All petri dishes were placed into an incubator at 25°C, with a 14-h light, 10-h dark photoperiod.

Larvae were checked daily for development. Emergence dates were recorded and the adults were removed, gender recorded, killed by freezing, oven dried at 60°C for 24 h, and weighed. The number of larvae successfully completing development to the adult stage (that is, survival), the mean number of days to adult emergence, and the weights of emerging male and female adults were then determined for each treatment.

The first bioassay indicated that larval development rate was reduced by sugar maple more than any other treatment. We hypothesized that larvae developed poorly on sugar maple leaves either because they are a poor quality food or, alternatively, solutes leached from the leaves negatively affect development. We conducted a second bioassay to assess these competing hypotheses. For these tests, we soaked 24 replicates of 0.4 g dried sugar maple leaves in 40 ml of deionized water for 2 weeks (as described above). The first treatment ($n = 6$) consisted of sugar maple leaves conditioned as in the first bioassay. For the second treatment, conditioned leaves were removed and added to new petri dishes containing fresh deionized water ($n = 6$). This treatment assessed whether the quality of leaves as mosquito food could be enhanced if water-soluble chemicals were removed. The third treatment used the conditioning water from treatment number two, with added dog food plus yeast ($n = 6$). This treatment assessed whether larvae supplied with unlimited food could still develop normally in the presence of chemicals leached from maple leaves. The fourth treatment was the control ($n = 6$) and consisted of deionized water and dog food plus yeast. As in the first assay, five larvae were added to each of the petri dishes and incubated. Larval survival, developmental time, and dry mass at emergence were measured as above.

Statistical Analysis

Single-factor analysis of variance was used to test for species or species-group (upland, wetland) differences in gravity input of litter (separately by year and wetland location), lateral litter flux, C/N ratios of upland and wetland litter, and C/N ratios of sugar maple, black ash, and trembling aspen (separately by year). For the last test, planned orthogonal contrasts were used to test for difference between (1) ash litter and pooled upland litter (maple and aspen) and (2) maple versus aspen litter.

For the breakdown experiment, natural log of percentage ash-free dry mass remaining was regressed on length of exposure in days to determine k, the processing coefficient, from the negative slope of the regression line (Olson 1963; Chen and others 2002). Regressions were run separately for each wetland to determine a mean k by species and location (margin, center). Regression r^2 values ranged from 0.52 to 0.96, with a mean (±sd) of 0.83 ± 0.12. All but two (of 24) regressions were significant ($P < 0.05$). Then a two-factor analysis of variance, where one factor was wetland location (margin, center) and the second factor was species (sugar maple, ash, aspen), was used to compare k rates for main effects and their interaction (species × location). Orthogonal contrasts were used to test for difference in breakdown rates between (1) ash litter and pooled upland litter (maple and aspen) and (2) maple and aspen litter.

The feeding bioassays were analyzed using single-factor analyses of variance. Treatments in the first analysis consisted of food type (control, black ash, sugar maple, trembling aspen leaves). Orthogonal contrasts were used to test for difference in mosquito larvae development rate, percent survival, and male and female weights between (1) control and pooled litter (ash, maple, aspen), (2) ash litter and pooled upland litter (maple, aspen), and (3) aspen and maple litter. Treatments in the second analysis consisted of the (1) control, (2) dog food plus yeast with sugar maple leachate, (3) sugar maple leaves in deionized water, and (4) sugar maple in leachate. For this test, Tukey's HSD test was used to assess pair-wise differences in larval response variables (as above), rather than planned contrasts, because we had no a priori assumptions about treatment differences.

Assumptions of normality and homogeneous variance were met with untransformed data in most comparisons. However, percent survival data in bioassays 1 and 2 were arcsine transformed and days to emergence from bioassay 1 were square-root transformed to better meet statistical assumptions (Sokal and Rolhf 1981). All statistical analyses were performed in SAS (SAS Institute 1989).

Results

Litter Flux

Mean (±1 SE) gravity input of litter into the wetlands (average among all locations in a wetland) was similar in both years, averaging 274 ± 38 g m^{-2} y^{-1} in 1997 and 252 ± 31 g m^{-2} y^{-1} in 1998. The distribution of these inputs between the wetland center and the margins was approximately equal in both years. However, upland species contributed significantly more litter into wetland margins than did

Table 1. Percent Composition of Total Biomass for Litter Entering Seasonal Wetlands

	Gravity Input		Lateral Input
Category	1997	1998	1998
Upland leaves			
Sugar maple (*Acer saccharum*)	15.6 ± 14.7	12.0 ± 4.2	26.2 ± 4.0
Trembling aspen (*Populus tremuloides*)	4.9 ± 0.8	5.2 ± 3.6	5.6 ± 1.7
Paper birch (*Betula papyrifera*)	6.5 ± 3.3	7.0 ± 1.8	5.4 ± 1.3
Northern red oak (*Quercus rubra*)	4.3 ± 3.6	2.4 ± 2.6	2.9 ± 1.4
Red maple (*Acer rubrum*)	3.3 ± 1.2	4.0 ± 3.2	14.3 ± 3.6
Basswood (*Tilia americana*)	2.7 ± 1.4	2.9 ± 2.4	3.9 ± 1.4
Other leaves	7.3 ± 4.2	12.1 ± 6.2	18.4 ± 3.5
Total upland leaves	44.7 ± 16.3	45.6 ± 14.0	76.7 ± 4.5
Upland twigs	17.0 ± 25.7	1.7 ± 1.3	0.0 ± 0.0
Upland seed/cones/flowers	4.0 ± 2.0	5.3 ± 3.1	2.3 ± 1.1
Wetland leaves			
Black ash (*Fraxinus nigra*)	23.3 ± 18.0	29.2 ± 10.1	17.9 ± 4.7
Other leaves	0.6 ± 0.6	0.6 ± 0.2	0.8 ± 0.3
Total wetland leaves	23.9 ± 18.0	29.8 ± 10.2	18.6 ± 4.6
Wetland twigs	0.04 ± 0.05	0.4 ± 0.4	0.0 ± 0.0
Wetland seed/cones/flowers	0.2 ± 0.3	1.3 ± 1.0	0.5 ± 0.2
Unknown	10.3 ± 3.4	15.5 ± 5.6	1.9 ± 0.8

Values are means ± 1 standard error (n = 4).
Other upland leaves include bigtooth aspen (Populus grandidentata)*, yellow birch* (Betula alleghaiensis)*, bur oak* (Quercus macrocarpa)*, balsam fir* (Abies balsamea)*, eastern white pine* (Pinus strobes)*, ironwood* (Ostrya virginiana).
Other wetland leaves include balsam poplar (Populus balsamifera)*, American elm* (Ulmus americana)*, speckled alder* (Alnus rubra).
Unknown category includes leaves, twigs, bark, and miscellaneous debris.

wetland species (1997: upland species = 202 ± 41 g m^{-2} y^{-1}, wetland species = 78 ± 49 g m^{-2} y^{-1}, $P = 0.008$; 1998: upland species = 207 ± 39 g m^{-2} y^{-1}, wetland species = 86 ± 57 g m^{-2} y^{-1}, $P = 0.003$). Gravity input of litter into wetland centers was not significantly different between upland and wetland sources in 1997 (119 ± 32 g m^{-2} y^{-1}, 150 ± 72 g m^{-2} y^{-1}, respectively) and 1998 (123 ± 42 g m^{-2} y^{-1}, 152 ± 81 g m^{-2} y^{-1}, respectively). In 1998, upland species contributed a significantly greater proportion ($P = 0.013$) of litter to lateral flux (42 ± 23 g m^{-1} y^{-1}) than did wetland species (4 ± 2 g m^{-1} y^{-1}).

The composition of litter collected in gravity traps was dominated by tree leaves (Table 1). Averaged over the 2 years, leaves of upland tree species comprised approximately 45% of total litter biomass, whereas leaves of wetland tree species contributed another 27% (Table 1). The remainder of litter biomass consisted of twigs and reproductive parts from a variety of upland and wetland woody species, as well as unidentified leaves, twigs, bark, and debris (Table 1). Lateral litter flux consisted largely of upland tree leaves (77% of total biomass), with sugar maple being the dominant species (26%). Black ash leaves comprised another 18% of the total (Table 1).

Litter Quality

Carbon to nitrogen ratios of pooled upland leaf litter were significantly higher than for pooled wetland derived litter in 1997 and 1998 ($P = 0.034$ and 0.003, respectively) (Table 2). Among species, C/N ratios of sugar maple, trembling aspen, and black ash leaf litter differed significantly in both 1997 and 1998 ($P = 0.002$ and 0.050, respectively) (Table 2). In both 1997 and 1998, the C/N ratio of ash litter was significantly lower than the pooled upland species ($P = 0.01$and 0.050, respectively). Ratios for sugar maple and aspen differed significantly in 1997 ($P = 0.004$), but not in 1998.

Leaf Litter Breakdown

Temporal patterns of litter breakdown differed among tree species (sugar maple, trembling aspen, black ash) and between locations within a wetland (Figure 1). In both locations (wetland center, margin), the rate of mass loss for ash litter became greater than the other two species sometime after 28 days, but before 204 days. This rate of mass loss was higher for ash in the wetland margins compared to the wetland centers, after approximately 200 days of exposure. After nearly one-year, ash

Table 2. Carbon to Nitrogen Ratios of Upland and Wetland Leaf Litter Entering Seasonal Wetlands

Category	1997	1998
Upland leaves		
Sugar maple (*Acer saccharum*)	71.3 ± 1.6	62.3 ± 0.7
Trembling aspen (*Populus tremuloides*)	55.9 ± 3.7	53.4 ± 6.2
All Upland leaves	66.6 ± 2.7	61.2 ± 2.0
Wetland leaves		
Black ash (*Fraxinus nigra*)	52.4 ± 2.7	47.5 ± 1.7
All Wetland leaves	50.9 ± 3.1	44.4 ± 2.5

Values are means ± 1 standard error (n = 4).
Additional upland leaf species include bigtooth aspen (Populus grandidentata), *yellow birch* (Betula alleghaiensis), *bur oak* (Quercus macrocarpa), *balsam fir* (Abies balsamea), *eastern white pine* (Pinus strobes), *ironwood* (Ostrya virginiana).
Additional wetland leaf species include balsam poplar (Populus balsamifera), *American elm* (Ulmus americana), *speckled alder* (Alnus rubra).

litter had lost approximately 66% of original mass in the wetland center and 82% of original mass in the wetland margin. Aspen litter lost approximately 43 and 48% of original mass in the wetland centers and margins, respectively, whereas maple litter lost 52 and 59% of original mass in wetland centers and margins, respectively.

Mean rates of leaf litter breakdown, as measured by *k*-values, differed by species and location (Figure 2). The interaction between species and location was not significant, so we examined species differences by pooling across locations, as well as location differences by pooling across species. The overall species difference in breakdown rates was significant ($P > 0.0001$). Black ash litter decomposed at a faster rate than upland species ($P < 0.0001$; Figure 2), whereas breakdown rates for maple and aspen litter did not differ significantly. Breakdown rates pooled across species were significantly faster at the wetland margin and then in the wetland center ($P = 0.0008$).

Feeding Bioassays

Survival rates of *Aedes aegypti* larvae exhibited a non-significant trend of progressive decline (Figure 3) from the control (>90% survival), to black ash litter (76%), to trembling aspen litter (71%), to sugar maple litter (60%). Days to emergence to an adult stage differed significantly among food sources, following a reverse order as survival ($P < 0.0001$; Figure 3). Days to emergence was lower for larvae reared on the control compared to leaf litter

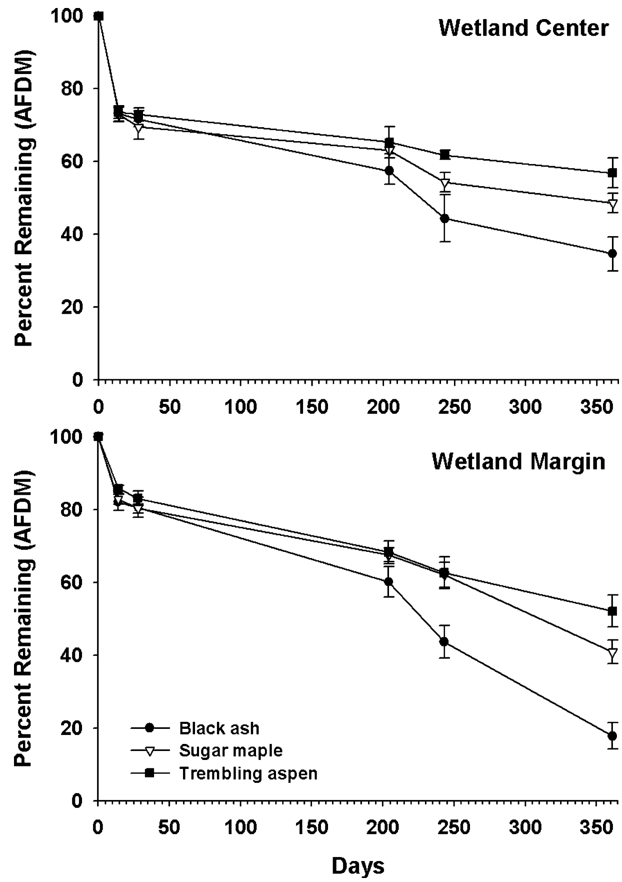

Figure 1. Average ash-free dry mass (AFDM) loss of leaves (±se) in seasonal wetlands (*n* = 4).

diets ($P < 0.0001$). Days to emergence for larvae reared on ash leaves was higher than on the control, but significantly less than larvae fed the pooled upland species ($P = 0.013$). Finally, days to emergence for larvae fed aspen leaves did not differ significantly than for those fed maple leaves.

The body mass of both male and female adult mosquitoes at the time of emergence differed among food sources ($P < 0.0001$). However, the differences largely stemmed from significantly greater mass ($P < 0.0001$) for larvae reared on the control, compared to leaf diets. Neither female nor male adult mass at emergence differed significantly between ash and pooled upland species or between aspen and maple.

In the sugar maple bioassay, similar survival rates (<20%) were observed in larvae fed sugar maple leaves leached of water-soluble chemicals and intact sugar maple leaves in the presence of leachate ($P > 0.05$; Figure 4). Similar survival rates (>90%) were also observed in larvae raised on dog food plus yeast in both deionized water (control) and water containing leachate from sugar maple leaves ($P >$

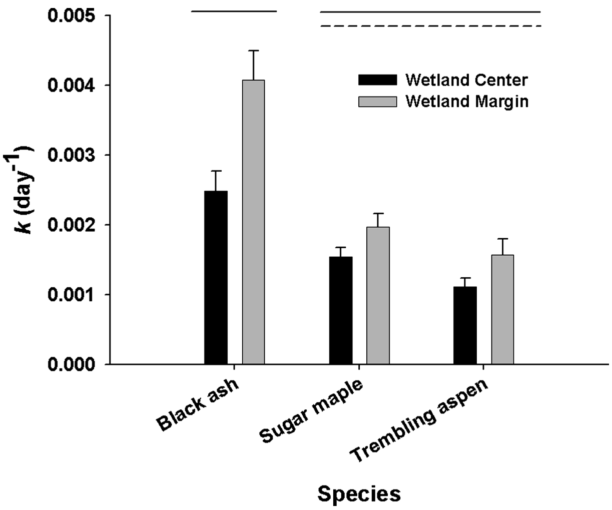

Figure 2. Average leaf litter processing coefficients (*k*) (±se) for three tree species by location within the wetland ($n = 4$). *Lines above bars* represent the results from two orthogonal contrasts: (*solid line*) black ash leaves versus aspen plus maple leaves; and (*dashed line*) aspen leaves versus maple leaves. For each contrast, values for bars underneath a contiguous line were not significantly different ($P > 0.05$).

0.05; Figure 4). However, survival rates were significantly higher ($P < 0.01$; Figure 4) in both of the former treatments (treatments not containing leaves) than in the latter treatments (those containing sugar maple leaves). We did not analyze days to emergence or body mass in this assay because so few larvae emerged for the treatments that included sugar maple leaves (Figure 4).

Discussion

Litter flux

The composition of litter falling into the seasonal wetlands we examined was dominated by upland tree species. Near the margins of the wetlands, upland species comprised over 70% of litter flux, and even more when lateral litter flux was considered. In this respect, seasonal wetlands are similar to headwater streams, where allochthonous litter from the surrounding upland forest is the primary source of plant organic matter in the system (Vannote and others 1980). A key distinction between seasonal wetlands and headwater streams is that emergent macrophyte production is much greater in the former. This can result in an increased input of wetland derived litter, which in our study contributed about 50% of total flux at the center of the wetlands. However, the impor-

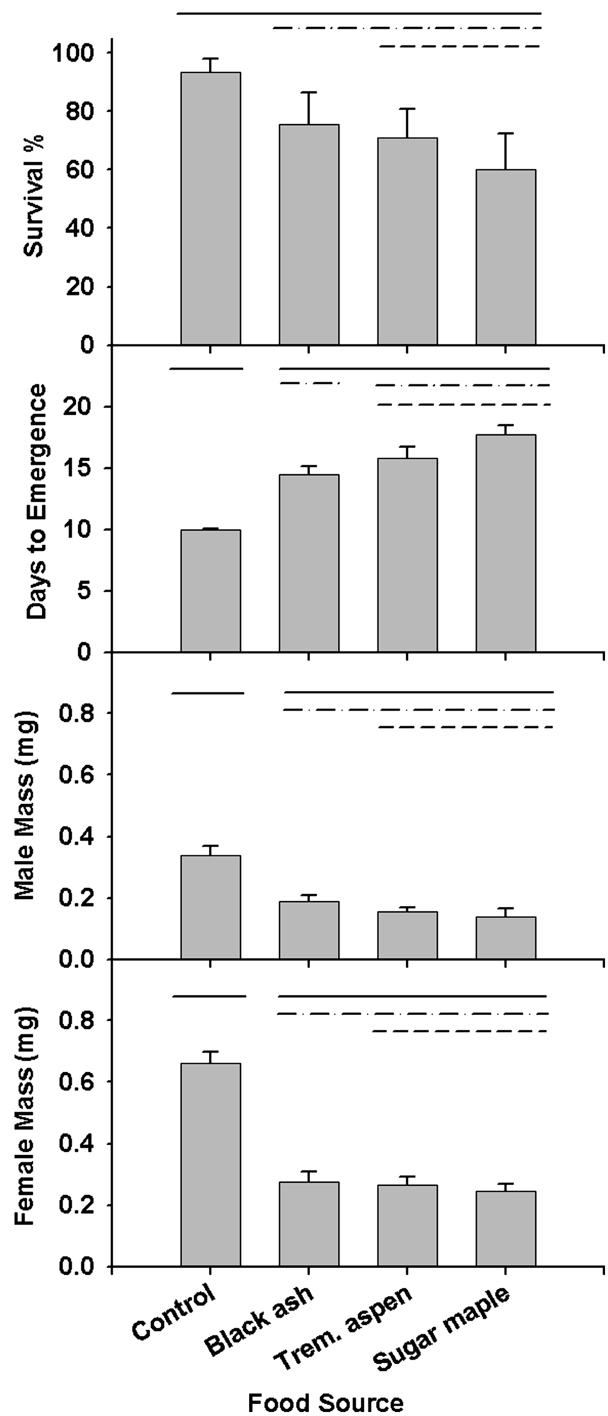

Figure 3. Developmental responses of *Aedes aegypti* larvae reared on diets of commercial dog food plus yeast (control) or leaves from black ash, sugar maple, and trembling aspen trees. Values are means (±se) of $n = 9$ replicates. *Lines above bars* represent the results from three orthogonal contrasts: (*solid line*) control versus leaf diets; (*dot-dashed line*) black ash leaves versus aspen plus maple leaves; and (*dashed line*) aspen leaves versus maple leaves. For each contrast, values for bars underneath a contiguous line were not significantly different ($P > 0.05$).

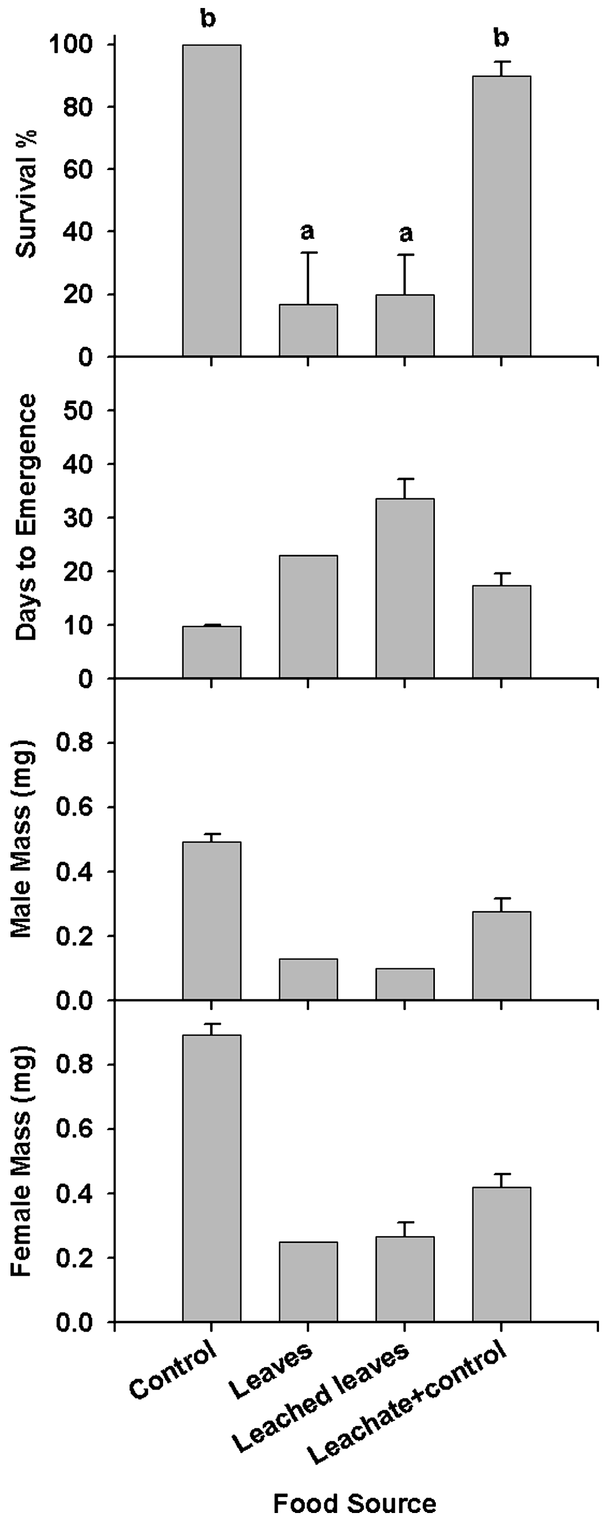

Figure 4. Development of *Aedes aegypti* larvae reared on diets of commercial dog food plus yeast (control), intact sugar maple leaves (leaves), sugar maple leaves leached of solutes (leached leaves), and commercial dog food plus yeast with extract solution from treatment 3 (leachate + control). Values are means (±se) of $n = 6$ replicates. *Bars* with the same letters were not significantly different ($P > 0.05$).

tance of this source of litter appears to be a function of size and perimeter to area ratio of these wetlands. The wetlands we examined were largely edge habitat, lacking a central core free from upland influence, at least in terms of litter flux.

Litter Quality and Breakdown

The abundance of upland litter in the wetlands may have important consequences for ecosystem processes, including litter breakdown, nutrient mineralization, and carbon assimilation into invertebrate foodwebs. Although a suite of environmental (temperature, moisture) and chemical factors (for example, lignin and cellulose concentrations, nutrient concentrations, lignin to nitrogen ratio, carbon to nitrogen ratio) control litter breakdown (Murphy and others 1998), generally, litter having high C/N ratios decomposes slower than litter with lower C/N ratios (Melillo and others 1982). In our study, leaves from sugar maple, the dominant upland species, and trembling aspen, a dominant in early successional forests of the study area, had significantly higher C/N ratios than leaves of black ash, the dominant wetland litter species.

Our breakdown data further supports this, with sugar maple and trembling aspen leaves (higher C/N) decomposing at a slower rate than black ash leaves (lower C/N), which has also been observed in another study (Petersen and Cummins 1974). Additionally, our data indicate that leaf litter breakdown rates were significantly faster near the margins of the wetlands, compared to the centers. This result may be due to the alternation of wet and dry conditions that occur near the margins and tend to increase litter breakdown rate, compared to longer periods of inundation in the wetland centers, which may slow breakdown (Shure and others 1986; Lockaby and others 1996).

Although we did not measure nutrient mineralization, it is plausible that differences in C/N ratios and breakdown rates between upland and wetland species will have measurable effects on nutrient processing in wetland soils. For instance, studies in upland forests demonstrate that nitrogen mineralization rates increase with increasing proportion of high quality litter in species mixtures (Finzi and Canham 1998). We hypothesize that all other conditions being equal, nitrogen mineralization rate will be higher in the center of wetlands (during dry phases), where higher quality black ash litter is abundant, compared to wetland margins, where poorer quality upland litter dominates.

Invertebrate Food Quality

The results of our feeding bioassays paralleled rates of litter breakdown. Development of *Aedes aegypti* mosquito larvae fed black ash leaves was significantly faster than for larvae fed aspen and maple leaves. Although black ash leaves were not optimal diets for the larvae, most larvae did complete development on these leaves. Notably, our results suggest that sugar maple leaves are a very poor quality food for *A. aegypti* larvae. Forty percent of larvae raised on sugar maple leaves died, and survivors had the slowest developmental rate of any treatment.

The problem with sugar maple leaves may have been related to the quality of the leaves as food rather than the occurrence of toxic secondary plant compounds (phenolics, alkaloids) in those leaves. Larvae fed sugar maple leaves faired poorly whether water-soluble chemicals were present or not. Larvae fed dog-food-plus-yeast had similar development whether or not chemicals leached from sugar maple leaves were present in the rearing water.

The higher C/N ratio of sugar maple leaves at the time of abscission likely resulted in lower rates of microbial colonization, slower breakdown rates, and thus lower nutritional quality for invertebrates. It appears that, compared to black ash leaves, sugar maple leaves are a poor food source for invertebrates in these seasonal wetlands. If the index of response developed using *A. aegypti* larvae reflects the response of invertebrates naturally occurring in the wetlands, it suggests that wetlands that receive an abundant supply of sugar maple leaves might be lower quality habitats for detritivorous invertebrates compared to wetlands that receive litter inputs dominated by black ash leaves or a mixture of black ash and aspen leaves. However, we caution against over extending our results without data from the full range of native invertebrate species.

Spatial and Temporal Availability of Conditioned Litter

The decreasing flux of upland litter into the wetlands, from the margins to the center, along with difference in breakdown rates among species and between wetland locations (for black ash), may result in temporal and spatial shifts in invertebrate community composition, densities, or biomass within the wetland. In streams, litter-consuming invertebrates (for example, shredders) require conditioned plant material that is leached of soluble chemicals and fully colonized by microbes, and as such, they do not key in on particular plant species, but rather on the condition of the litter (Cummins and others 1989). In seasonal wetlands, litter-consuming invertebrates must complete development in a short period, and thus targeting foods of the highest quality might be especially important (Wissinger 1999). It may be that during the spring to early summer inundation period, invertebrate activity shifts to capitalize on changing abundance of conditioned litter within different locations of wetlands, for example, black ash near the margins, followed by black ash in wetland centers, and finally, upland litter in both locations.

Conclusions

Our results demonstrate that leaf litter inputs from upland forests can significantly influence organic matter dynamics of small seasonal wetlands. This can in turn influence ecological processes within that wetland. For instance, significant inputs of low quality leaf litter (for example, sugar maple, trembling aspen) from an upland forest could lower nutrient mineralization rates or carbon assimilation by wetland invertebrates compared to a litter pool dominated by higher food quality litter (for example, black ash). Alternatively, if the upland forest is dominated by species with higher quality litter, then there may be corresponding increases in litter breakdown rates or feeding efficiencies of wetland invertebrates.

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